

The Earliest Shrew (Soricidae, Mammalia) from the Middle Eocene of Mongolia

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Abstract—The earliest and most primitive shrew, *Soricolestes soricavus* gen. et sp. nov. from the Middle Eocene Khaychin Formation of the Khaychin-Ula II locality, Mongolia, is described. *Soricolestes* has typical soricid lower molars and is characterized by well-differentiated antemolars, a large and semimolariform P₄, the presence of the hypoconulid on M₃, a long and low mandible, a deep masseteric fossa, and a superficial internal temporal fossa. The structural features of the lower jaw, antemolars, P₄, and M₃ show that *S. soricavus* should be ranked as a separate subfamily, Soricolestinae subfam. nov.

INTRODUCTION

Shrews (Soricidae) compose the most specialized insectivore group, perfectly adapted for feeding on small invertebrates. In the Recent fauna, the Soricidae are widespread and occur almost everywhere (except for Australia, certain regions of South America, and polar regions); they inhabit various landscapes and lead terrestrial, underground, and semiaquatic modes of life. The Soricidae substantially contribute to the species diversity of the extant Insectivora; there are about 335 shrew species (23 genera) (Wolsan and Hutterer, 1998), i.e., approximately 80% of the total number of insectivore species. Fossil remains of more than 250 (about 200 extinct and 50 extant) species from more than 70 (about 60 extinct and 13 extant) genera have been described (Wolsan and Wójcik, 1998).

The diversity of the Recent shrew groups developed in the Late Miocene and Pliocene (Repenning, 1967; Rzebik-Kowalska, 1997, 1998; Storch *et al.*, 1998). In the Neogene, the Soricidae were represented by the following six subfamilies: the extinct Heterosoricinae, Crocidosoricinae, Limnoecinae, and Allosoricinae and the Recent Soricinae and Crocidurinae. In the Oligocene, only the Heterosoricinae and Crocidosoricinae were found. The subfamily Heterosoricinae, existing from the end of the Middle Eocene to the onset of the Pliocene, is considered to be the most primitive shrew group. Some researchers rank it as a family (Reumer, 1987, 1998). The earliest known soricid genus, *Domnina* Cope, 1873, from the Middle Eocene–Early Miocene of North America (McKenna and Bell, 1997; Harris, 1998), belongs to the Heterosoricinae. In the Middle Eocene, *Domnina* is known from the Late Uintan and Duchesnean (Stucky, 1992); the Late Uintan forms were determined as *D. cf. D. gradata* Cope, 1873 (Krishtalka and Setoguchi, 1977) and *Domnina* sp. (Storer, 1984).

In Europe, the earliest Soricidae are known from the Lower Oligocene; *Quercysorex* sp. (Heterosoricinae) comes from MP21 and *Srinitium* cf. *marteli* Huguene, 1976 (Crocidosoricinae) is from MP22 (Ziegler and Heizmann, 1991; Rzebik-Kowalska, 1998). The appearance of shrews in Europe is probably associated with mass immigration of Asian mammals at the Eocene–Oligocene boundary.

The earliest known shrew from Asia is *Gobisorex kingae* Sulimski, 1970 (Heterosoricinae) from the Early Oligocene Shand-Gol Fauna of Mongolia (Sulimski, 1970; Storch *et al.*, 1998). *Gobisorex* cf. *kingae* was registered in the Early Oligocene Buran Fauna of eastern Kazakhstan (Gabunia and Gabunia, 1987).

Cretasorex arkhangel'skyi Nesson et Gureev, 1981 from Uzbekistan, originally dated as the Late Cretaceous (Nesson and Gureev, 1981), is presently considered to be a Late Cenozoic form (Nesson *et al.*, 1994; Storch *et al.*, 1998).

Wang and Li (1990) described *Ernosorex jilinensis* from the Middle Eocene of China and assigned it to the Soricidae. Subsequently, *Ernosorex* was combined with the genera *Changlelestes*, *Tupaiodon*, and *Ictopidium* in the family Changlelestidae, assigned to the Soricomorpha (Tong and Wang, 1993). In actual fact, *Tupaiodon*, *Ictopidium*, and *Changlelestes* belong to the Erinaceidae, whereas *Ernosorex* belongs to the Plesiosoricidae (Storch and Dashzeveg, 1997; McKenna and Bell, 1997).

The present study considers a Middle Eocene insectivore, the molar structure of which clearly shows that it is a member of the Soricidae. The material is fragmentary lower jaws from the Khaychin Formation of the Khaychin-Ula II locality, Mongolia, which was collected by the South Gobi Party of the Joint Soviet–Mongolian Paleontological Expedition headed by V. Yu. Reshetov in 1971–1973 and stored at the Paleon-

tological Institute of the Russian Academy of Sciences (PIN).

The Khaychin-Ula II locality is dated to the Middle Eocene (Badamgarav and Reshetov, 1985; Russell and Zhai, 1987) or the end of the Middle or beginning of the Late Eocene (Devyatkin, 1981, 1994). I adhere to the first point of view. Averianov and Godinot (1998) estimated the age of this locality as the Early Lutetian. The Khaychin-Ula II Fauna belongs to the Irindmanhan Asian Land Mammal Age, which is correlated with the Early–Middle Uintan of North America (McKenna and Bell, 1997). Consequently, the shrew described below is substantially older than the previously known North American Soricidae, dated to the Middle Eocene.

When describing the dental structure, I use the terminology proposed by Hutchison (1974). The dental formulas are given in both the form traditional for mammals (number of incisors, canines, premolars, and molars) and the form commonly used for the Soricidae (anterior incisor, the number of antemolars, P₄, and the number of molars).

SYSTEMATIC PALEONTOLOGY

Family Soricidae Fischer, 1817

Subfamily Soricolestinae Lopatin, subfam. nov.

Type genus. *Soricolestes* gen. nov.

D i a g n o s i s. Small archaic shrews with differentiated lower antemolars and dental formula I₃C₁P₃M₃ (1.5.1.3). P₄ large and semimolariform: with low paracoid, high protoconid, rudimentary metaconid, and well-developed and unicuspid talonid. M₁ ≥ M₂ > M₃. Entostylid of M₁ and M₂ large and well developed. M₃ with hypoconulid, postcrisid isolated from entocoid. Horizontal ramus of mandible long and low. Mental foramen under P₃. Ascending ramus long, masseteric fossa large and deep, external temporal fossa absent, and internal temporal fossa superficial and not pocketed.

C o m p o s i t i o n. Type genus.

C o m p a r i s o n. The Soricolestinae differ from the Heterosoricinae Viret et Zapfe, 1951; Crocidosoricinae Reumer, 1987; Soricinae Fischer, 1817; Crocidurinae Milne-Edwards, 1868; Limnoecinae Repenning, 1967; and Allosoricinae Fejfar, 1966 by the presence of well-differentiated antemolars, the structure of P₄ and M₃, and a long ascending ramus of the mandible with a poorly developed internal temporal fossa. In addition, the new subfamily differs from all listed subfamilies, except for the Heterosoricinae, by the presence of the masseteric fossa and the unpocketed internal temporal fossa. The dental formula is more complete; the number of antemolars is greater by at least one tooth than that in the other Soricidae (except for *Srinitium* Huguene, 1976); the entostylid on M₁ and M₂ is better developed; and the mental foramen is more anteriorly positioned.

Genus *Soricolestes* Lopatin, gen. nov.

E t y m o l o g y. From the generic name *Sorex* and the Greek *lestes* (robber).

T y p e s p e c i e s. *Soricolestes soricavus* sp. nov.

D i a g n o s i s. Type genus of a monotypic subfamily.

C o m p o s i t i o n. Type species.

Soricolestes soricavus Lopatin, sp. nov.

E t y m o l o g y. From the generic name *Sorex* and the Latin *avus* (ancestor).

H o l o t y p e. PIN, no. 3107/405, fragmentary right mandible with P₄–M₃ and alveoli of C₁–P₃; Mongolia, Khaychin-Ula II; Middle Eocene, Khaychin Formation.

D e s c r i p t i o n (Figs. 1–3). The horizontal ramus of the mandible is extended and very low; its height is less than that of M₁ or M₂ and only a little greater than that of M₃. The lower edge of the bone is weakly curved. The lower region of the labial surface is usually flattened at the level of the molars (Figs. 2d, 3m). The mental foramen is large and located under P₃. Occasionally, the labial side of the jaw contains a very small supplementary foramen under the interval between M₂ and M₃ (Fig. 2d); the foramen faces posteriorly and is positioned in a short and narrow groove. The symphysis is weak and long and extends posteriorly to the level of the anterior root of P₄; at P₂, the lower part of the symphyseal region has a small anteromedially facing foramen (foramen postsymphyseale).

The distance between M₃ and the base of the coronoid process is approximately equal in length to M₃. The angle between the coronoid process and the horizontal ramus is approximately 110°–115°. At the incisure between the articular and angular processes (lower sigmoid incisure), the ascending ramus is equal in length to the distance between the anterior edge of M₂ and the base of the coronoid process. The coronoid process is high, more than 2.5 times as high as the horizontal ramus. The dorsal part of the coronoid process is very short and acutely angled, and its posterior side is positioned almost vertically. The masseteric fossa is deep; anteriorly, it is limited by a stout ridge rising almost to the apex of the coronoid process. In the anteroventral angle of the masseteric fossa, the bone surface is rough and has one to several tiny pits. The internal temporal fossa is superficial; the ridge at its base is sharp and well-developed; in the posterior part, the ridge ascends dorsally. The mandibular foramen is large, located on a level with the upper edge of the horizontal ramus, and strongly displaced posteriorly close to the lower sigmoid incisure. This incisure is wide, and its height gives evidence that the articular condyle was located higher than the apices of the molar cusps. The lower edge of the ascending ramus strongly curves dorsally. The base of the angular process is posteroventrally directed.

Judging from the alveoli (Figs. 1c, 3a, 3b), I₁ was a relatively large, extended, and anteriorly directed tooth;

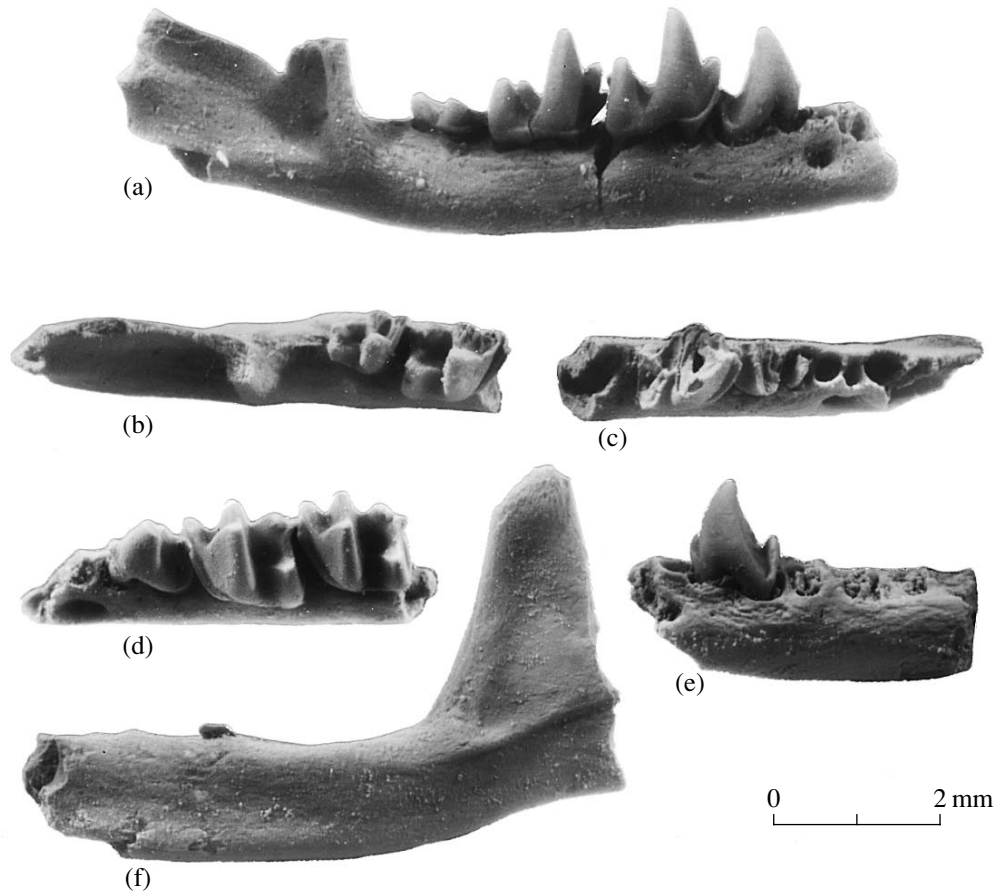


Fig. 1. *Soricolestes soricavus* sp. nov.: (a) holotype PIN, no. 3107/405, fragmentary right dentary with P₄–M₃, labial view; (b) specimen PIN, no. 3107/408, fragmentary right dentary with M₂ and M₃, occlusal view; (c) specimen PIN, no. 3107/409, fragmentary right dentary with damaged P₄ and M₁ and alveoli of I₁–P₃, occlusal view; (d) specimen PIN, no. 3107/406, fragmentary left dentary with P₄–M₂, occlusal view; (e) specimen PIN, no. 3107/407, fragmentary left dentary with P₄, labial view; and (f) specimen PIN, no. 3107/410, fragmentary right dentary, lingual view.

I₂ and, especially, I₃ were strongly reduced. The I₁, I₂, and I₃ alveoli are inclined in relation to the horizontal ramus at angles of approximately 10, 20, and 30°, respectively. The I₃ alveolus is labially displaced. The canine alveolus is relatively large, round, and inclined at an angle of about 40°. Between the canine alveolus and P₄, there are two small alveoli, which presumably contained single-rooted P₂ and P₃. The P₂ alveolus is substantially smaller than the P₃ alveolus. Thus, the alveoli of single-rooted antemolars between I₁ and P₄ change in size as follows: C₁ > P₃ > P₂ > I₂ > I₃ (A₃ > A₅ > A₄ > A₁ > A₂).

P₄ is double-rooted, large, and high. The paraconid is small and basal and occupies the anterolingual position; occasionally, it is strongly reduced and virtually indiscernible in labial view. The precingulid is very short and weak or absent. The protoconid is high and conical or pyramidal and has a flat posterior wall. Its posterolingual and posterolabial angles form sharp edges; the lingual edge bears a small expansion, a rudimentary metaconid, which is located substantially lower than the apex of the protoconid. The talonid is

short and lacks posterior sulcus, and the lingual angle strongly projects posteriorly. A relatively high posterolingual cusp is present. A well-pronounced postcingulid extends along the posterolabial edge.

The shape of M₁–M₃ is typical of shrews; i.e., the trigonid is raised and the cusps are lingually oblique; on M₁ and M₂, the talonid is only slightly shorter and narrower than the trigonid.

M₁ is somewhat larger than M₂. The precingulid is well-developed and extends along the anterolabial side of the crown from the level of the paracristid notch to the level of the protoconid apex. The paraconid is relatively low. The paracristid abruptly curves anterolabially and has a distinct notch. The trigonid basin is relatively wide and deep. The entocingulid is very weak and is a poorly pronounced elevation at the interval between the paraconid and the metaconid. The protoconid and the metaconid are strongly longitudinally compressed and positioned close to each other, and the protoconid is substantially more massive and higher than the metaconid. The posterior wall of the trigonid is vertical. The hypoflexid is not very deep. The ectocin-

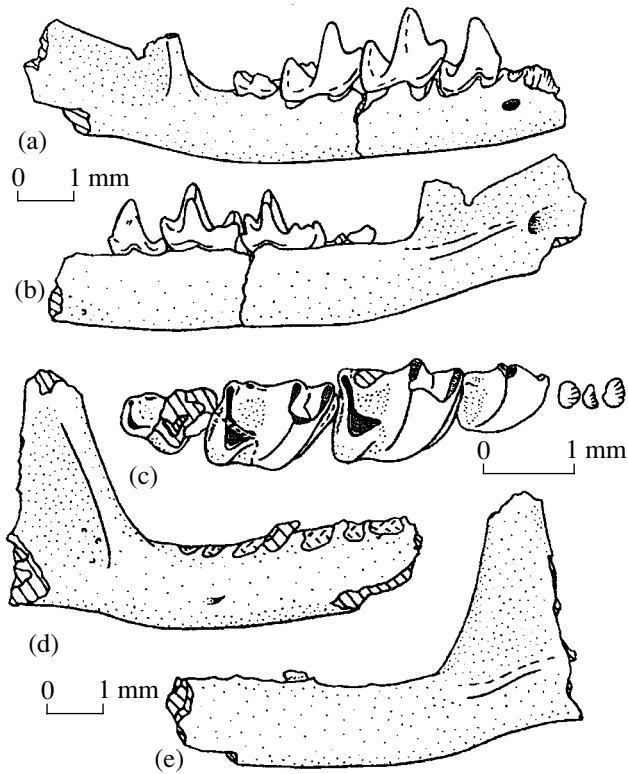


Fig. 2. *Soricolestes soricavus* sp. nov.: (a–c) holotype PIN, no. 3107/405, fragmentary right dentary with P_4 – M_3 : (a) labial view, (b) lingual view, and (c) alveoli and teeth, occlusal view; (d, e) specimen PIN, no. 3107/410, fragmentary right dentary: (d) labial view and (e) lingual view.

guld is very narrow and weak. The hypoconid is relatively large and strongly projects posterolabially. The cristid oblique reaches the middle of the base of the posterior wall of the protoconid. The entoconid is small and conical. The entocristid is well-pronounced and relatively high and lingually closes the talonid basin. The postcristid (hypolophid) is free and terminates in the entostylid. The entostylid is relatively large (only slightly smaller than the entoconid) and markedly projects posterolingually; however, it is low and isolated from the entoconid by a small postentoconid fold. The postcingulid is well developed and extends from the base of the posterior wall of the hypoconid to the entostylid.

M_2 is similar in morphology to M_1 ; however, it differs by smaller measurements and certain structural details. The precingulid is better developed and originates at the level of the paraconid apex. The paraconid is smaller, and the paracristid curves more gently. The trigonid basin is narrow, because the paraconid and metaconid are positioned close to each other. The entocingulid is indiscernible. The protocristid is longer, since the protoconid and the metaconid are positioned at a greater distance from each other. The hypoflexid is deeper and all cusps are less massive than those of M_1 .

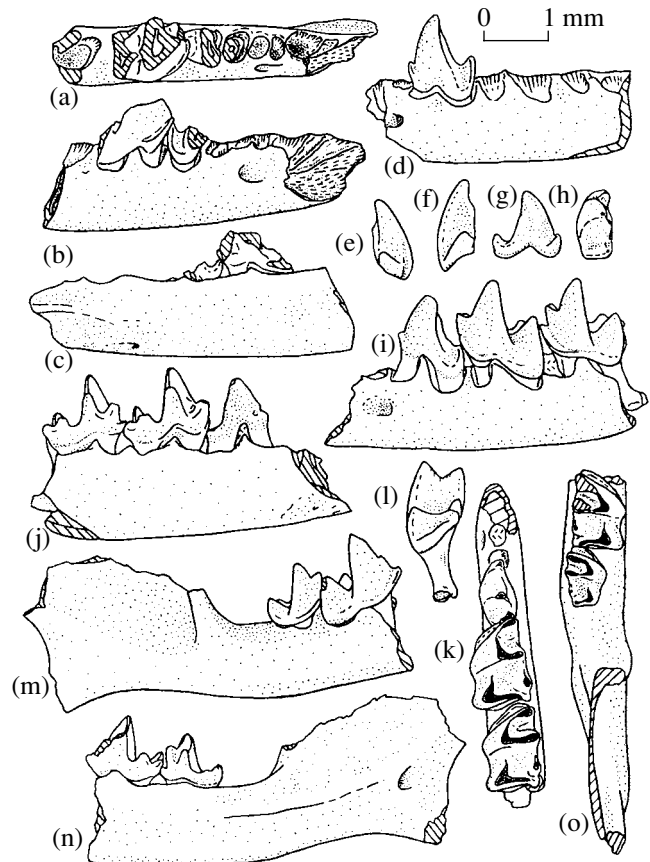


Fig. 3. *Soricolestes soricavus* sp. nov.: (a–c) specimen PIN, no. 3107/409, fragmentary right dentary with damaged P_4 and M_1 and alveoli of I_1 – P_3 : (a) occlusal view, (b) labial view, and (c) lingual view; (d–h) specimen PIN, no. 3107/407, fragmentary left dentary with P_4 : (d) labial view; (e) P_4 , frontal view; (f) P_4 , rear view; (g) P_4 , lingual view; and (h) P_4 , occlusal view; (i–l) specimen PIN, no. 3107/406, fragmentary left dentary with P_4 – M_2 : (i) labial view; (j) lingual view; (k) occlusal view; and (l) M_2 , rear view; (m–o) specimen PIN, no. 3107/408, fragmentary right dentary with M_2 and M_3 : (m) labial view, (n) lingual view, and (o) occlusal view.

M_3 is substantially smaller than M_2 . The trigonid is of the same structure as that of M_2 . The hypoflexid is deep and the ectocingulid is weak. The talonid is narrow; however, it is equal to or greater than the trigonid in length. The hypoconid is well-developed, and the cristid oblique is weak. The entoconid is extremely strongly reduced and fused with a relatively high entocristid, which lingually encloses the talonid basin. The hypoconulid is larger than the entoconid, separated from the latter by a well-pronounced postentoconid fold, and connected to the hypoconid by a short postcristid. The postcingulid is absent.

Measurements, mm. Holotype, length: P_4 – M_3 , 4.6; P_4 – M_2 , 3.7; P_4 – M_1 , 2.35; M_1 – M_3 , 3.7; M_1 – M_2 , 2.8; and M_2 – M_3 , 2.35. Specimen PIN, no. 3107/406, length: P_4 – M_2 , 3.6; P_4 – M_1 , 2.3; and M_1 – M_2 , 2.7. Specimen PIN, no. 3107/407, length: M_2 – M_3 , 2.37.

Alveoli of antemolars, length \times width: C₁, 0.55 \times 0.4; P₂, 0.2 \times 0.35; P₃: (PIN, no. 3107/409) 0.33 \times 0.35, (PIN, no. 3107/405, 406) 0.35 \times 0.3, and (PIN, no. 3107/408) 0.3 \times 0.3.

Measurements of the lower cheek teeth, L (L_{TL}) \times W_{TR}–W_{TL}, where L is the total length, L_{TL} is the talonid length, W_{TR} is the trigonid width, and W_{TL} is the talonid width:

Tooth	Holotype, PIN, no. 3107/405	no. 3107/406	no. 3107/407	no. 3107/408
P ₄	1.05 (0.3) \times 0.6–0.55	1.0 (0.25) \times 0.6–0.55	–	1.05 (0.3) \times 0.6–0.55
M ₁	1.35 (0.65) \times 1.0–1.0	1.38 (0.6) \times 0.9–0.95	–	–
M ₂	1.3 (0.6) \times 0.95–0.9	1.33 (0.6) \times 0.85–0.85	1.3 (0.6) \times 0.95–0.9	–
M ₃	~0.9 (0.4) \times ?–0.5	–	0.95 (0.45) \times 0.87–0.52	–

Height of the coronoid process (PIN, no. 3107/410), ca. 4.0.

Depth of the horizontal ramus, lingual side:

Level PIN	no. 3107/405	no. 3107/406	no. 3107/407	no. 3107/408	no. 3107/409	no. 3107/410
Under P ₂	1.15	–	–	–	1.25	–
Under P ₃	1.20	1.20	–	–	1.25	–
Under P ₄	1.25	1.25	–	1.25	1.25	–
Under M ₁	1.30	1.35	–	1.35	1.35	1.5
Under M ₂	1.25	1.40	1.30	1.30	1.40	1.45
Under M ₃	1.25	–	1.25	–	–	1.35
Behind M ₃	1.20	–	1.15	–	–	1.35

Material. In addition to the holotype, five fragmentary mandibles from the type locality: (PIN, no. 3107/406) with P₄–M₂ and alveolus of P₃; (PIN, no. 3107/407) with M₂, M₃, and a fragmentary ascending ramus; (PIN, no. 3107/408) with P₄ and alveoli of P₃, M₁, and M₂; (PIN, no. 3107/409) with poorly preserved P₄ and M₁ and alveoli of I₁–P₃; and (PIN, no. 3107/410) with the base of the trigonid of M₂, alveoli of P₄–M₃, and an almost complete coronoid process.

DISCUSSION

In 1967, Repenning reviewed the Soricidae known at that time (Repenning, 1967) and proposed that a hypothetical ancestor of all shrews should have the following characters (the characters of the upper teeth are omitted, and the terminology is adapted to that accepted in the present study): (1) the dental formula of the lower teeth is 1.4.1.3 (I₁, A₁–A₄, P₄, M₁–M₃); (2) the lower incisor is large and procumbent (directed anteriorly); (3) the lower antemolars have one triangular cusp, the anterior and posterior antemolars (P₄) are the largest, and the tooth row is only weakly compacted; (4) P₄ is nonmolariform, unicuspid, double-rooted, and has well-pronounced cingulids; (5) in M₁, the trigonid and talonid are well developed, the metaconid and paraconid are isolated to a greater extent than in M₂, the cristid oblique is connected to the trigonid in the middle of the tooth or to the metaconid, the entoconid is clearly

isolated from the postcristid (hypolophid) and connected to the metaconid by a high and well-developed entocristid, the hypoconulid is absent, the labial cingulid is stout, and the hypoflexid reaches the level of the ectocingulid; (6) M₂ is similar to M₁, but the paraconid is located closer to the metaconid; (7) the trigonid of M₃ is similar to that of M₂, but the talonid is reduced and the entoconid is connected to the postcristid; (8) the internal temporal fossa is extensive but not pocketed; (9) the mental foramen is under P₄ or P₃; and (10) the size of the animal is small. The above list contains characters common to all known Soricidae (1–8), mainly, in their most primitive state (1, 3–5, 7, and 8); in addition, it includes hypothetical characteristics of the primitive state (9 and 10) of certain characters.

Repenning believed that shrews originated from an unknown member of the Soricidae of the pre-Oligocene age (according to the modern concept, the pre-Late Eocene age). The discovery of the Middle Eocene Soricidae in North America did nothing to solve the problem of the origin of this family; Late Uintan *Domnina* cf. *D. gradata* from Wyoming (Krishtalka and Setoguchi, 1977, p. 91) and *Domnina* sp. from Saskatchewan (Storer, 1984, p. 44, fig. 4H) only slightly differ from the well known Late Eocene–Early Oligocene *D. gradata*; in particular, Harris even (1998) proposed that the form from Wyoming was conspecific to *D. gradata*.

Wang and Li (1990) considered *Ernosorex jilinensis* from the Middle Eocene of China as a presumable

Asian ancestor of the Soricidae. Similar to *Soricolestes*, this species has three incisors, one canine, three premolars, and three molars in the mandible (I_1 , I_2 , C_1 , P_4 , and M_1 are preserved). The anterior incisor of *Ernosorex* is very large and procumbent and has a bilobate crown; P_4 is large and has a rudimentary paraconid, a high pyramidal protoconid, and a short talonid (Wang and Li, 1990, fig. 7). However, the structure of M_1 (in particular, the presence of a relatively large hypoconulid located in the middle of the posterior edge of the talonid) substantiates the exclusion of this form from the Soricidae (McKenna and Bell, 1997; Storch *et al.*, 1998).

Soricolestes shows almost the entire set of characters proposed by Repenning for the hypothetical common ancestor of shrews. The formula of the lower teeth (1.5.1.3) differs from that given by Repenning; however, the presence of five single-rooted antemolars between the anterior incisor and P_4 is currently known in the Oligocene Crocidosoricinae of the genus *Srinitium* (Ziegler, 1998). The presence of a reduced paraconid and a rudimentary metaconid on P_4 , the absence of connection between the postcrisid and the entoconid on M_3 , and the absence of well-developed ectocingulid on P_4 – M_3 are the characters indicating that *Soricolestes* is more primitive than other shrews. The structure of M_1 and M_2 is in general so similar to the later Soricidae that, if *Soricolestes* were represented by only these teeth, it would be difficult to distinguish it from certain Oligocene and Miocene taxa.

It is important to consider in more detail some morphological features in high evolutionary significance of the lower jaw and teeth of *Soricolestes*.

Homology of the anterior lower incisor. The homology of the procumbent lower incisor of the Soricidae (the so-called soricid incisor, I_1 or I_2) is not known with certainty (Repenning, 1967; Butler, 1988); however, it is customary to assume this is I_1 (Gureev, 1979; Dannelid, 1998). The number, measurements, and arrangement of the alveoli of the anterior teeth of *Soricolestes* clearly demonstrate that the Soricidae initially had increased I_1 . This is evidence of the essential dissimilarity between the Soricidae and the Plesiosoricidae (having increased I_2), which are occasionally considered to be close to each other (Van Valen, 1967; Butler, 1988).

Number, differentiation, and homology of the antemolars. The small single-rooted teeth of the Soricidae that are located between I_1 and P_4 are usually named the intermediate teeth (Gureev, 1979) or antemolars (Repenning, 1967; Ziegler, 1998; Dannelid, 1998) and designated depending on their number as follows: A_1 , A_1 – A_2 , etc., up to A_1 – A_5 (Ziegler, 1998). The arrangement, orientation, and relative sizes of the five antemolar alveoli of *Soricolestes* allow one to identify the teeth from these alveoli as I_2 , I_3 , C_1 , and two premolars (presumably, P_2 and P_3). The same interpretation is probably applicable to A_1 – A_5 of *Srinitium caeruleum* Ziegler,

1998 from the Upper Oligocene of Germany (Ziegler, 1998). However, the antemolar alveoli of *Srinitium* are positioned closer to each other than those of *Soricolestes* and have approximately the same measurements and shape (Ziegler, 1998, pl. 6, fig. 77); this is associated with a greater shortening and monomorphy of the antemolar row.

As the premolar row of insectivores is reduced, P_1 is the first to disappear; it is therefore safe to assume that P_1 is the tooth that absent in *Soricolestes*. Since the I_3 and I_2 alveoli are the smallest alveoli of *Soricolestes*, it is most likely that, in the course of reduction of the antemolar row, advanced Soricidae first lost the third and second incisors. Of the two single-rooted premolars of *Soricolestes*, P_2 is smaller than P_3 ; therefore, in the evolution of the Soricidae, the former probably disappeared earlier than the latter. Thus, the sequence of reduction of the antemolars in shrew evolution is expressible as follows: P_1 – I_3 – I_2 – P_2 – P_3 . At the same time, this process could occur differently in different lineages; in particular, the A_1 alveolus of *Srinitium caeruleum* is substantially larger than the alveoli of the four other antemolars (Ziegler, 1998); consequently, I_2 did not show a tendency to reduction in the early Crocidosoricinae.

Structure of P_4 . With reference to the size and structure of the posterior premolar, *Soricolestes* significantly differs from the other Soricidae and resembles the Plesiosoricidae and some members of the Talpidae and Chiroptera. P_4 of *Soricolestes* is similar to P_4 of the Early Eocene nyctitheriid *Oedolius* from the Bumbanian Fauna of Mongolia (Russell and Dashzeveg, 1986, p. 276, figs. 5d, 5e) and the above-mentioned *Ernosorex*; however, it differs by the presence of a rudimentary metaconid. Repenning (1967) considered nonmolariform P_4 of shrews to be a primitive character; on this basis, he proposed that the Soricidae and Chiroptera are closely related and diverged as an integral lineage in the pre-Cenozoic from the insectivores that were characterized by molariform P_4 . Sigé (1976) has shown that the molariform structure of the posterior premolar is a primitive character of the Lipotyphla (and the Chiroptera), whereas simplified structural types of P_4 are characteristic of evolutionarily advanced groups and appeared as a result of parallel development. The semi-molariform structure of P_4 of *Soricolestes* combined with the reduced paraconid, rudimentary metaconid, and unicuspid talonid indicate that the specialized P_4 characteristic of late shrews was formed as a result of progressive demolarization of the posterior premolar of the early Soricidae.

Structure of the talonid of M_3 . In contrast to that in other shrews, in *Soricolestes* the talonid of M_3 has three cusps rather than one or two; moreover, the postcrisid (hypolophid) is detached from the reduced entoconid, as on the talonid of M_1 and M_2 . The structure of the talonid of M_3 of *Soricolestes* allows one to propose that, in the later Soricidae, the lingual cusp of the talonid of

M_3 is also the hypoconulid rather than the entoconid (as is customary to assume), while the true entoconid is included in the entocristid. The element designated as the entostylid of M_1 and M_2 of shrews is homologous to the hypoconulid (Sigé, 1976). It is formed as a result of displacement of the hypoconulid into the posterolingual corner of the occlusal surface combined with its connection to the hypoconid and primary isolation from the entoconid, as in nyctalodont chiropters (Menu and Sigé, 1971). In the course of soricid evolution, this element lost its initial cuspid shape and, subsequently (independently in different groups), was strongly reduced or completely disappeared (in the case where the postcristid was connected to the entoconid).

Position of the mental foramen. In the majority of shrews, the mental foramen is located under M_1 ; occasionally, it is under P_4 ; and in the advanced Heterosoricinae, it is displaced and positioned under M_2 (Repenning, 1967; Engesser, 1975). The position of the mental foramen under P_4 is characteristic of many Oligocene and Miocene genera of the Crocidosoricinae (Crochet, 1975; Ziegler, 1989, 1998). The more anterior position of this foramen in *Soricolestes* (under P_3) shows the general primitiveness of this form. The posterior displacement of the mental foramen in the course of shrew evolution is associated with an increase in the incisor size (Engesser, 1979); thus, one can propose that, in *Soricolestes*, the anterior lower incisor had only slightly increased.

Structure of the ascending ramus of the mandible. Unfortunately, the available material does not give data on the presence or absence in *Soricolestes* of the main autapomorphic feature of the Soricidae (Repenning, 1967; MacPhee and Novacek, 1993), the double articulation of the mandible with the skull, which is indicated by the presence of a double articular condyle containing separate upper and lower articular facets. However, the formation of the double jaw articulation of shrews is accompanied by a significant functional rearrangement of the jaw muscles, including the loss of a large part of the masseter and the displacement of a portion of the temporal muscle onto the medial side of the coronoid process (MacPhee and Novacek, 1993). As this process developed, in the majority of shrews, the masseteric fossa disappeared and the external and internal temporal fossae were formed. Therefore, the presence of a deep and large masseteric fossa on the coronoid process of the mandible of *Soricolestes* and the absence of a distinct internal temporal fossa are indirect evidence of the absence or underdevelopment of the double articular condyle.

Among shrews, only the Heterosoricinae have the masseteric fossa of the mandible. The internal temporal fossa of these animals is shallow and not pocketed. In *Soricolestes*, the masseteric fossa is more extensive and deeper than in the Heterosoricinae, whereas the internal temporal fossa is scarcely visible. The articular condyle of *Soricolestes* was probably more primitive than even

the condyle of *Domnina*, the facets of which were incompletely isolated from each other (Repenning, 1967, p. 8, fig. 2).

Another indirect evidence of the absence of a detached lower articular facet in *Soricolestes* is the absence of the posterior medial ridge; in other shrews, this ridge overhangs the mandibular foramen and extends to the articular condyle.

The high vertical coronoid process with an acute-angled apex that observed in *Soricolestes* is typical of the Soricidae. In the Nyctitheriidae, the coronoid process is usually longer, flat, and low, with a more rounded apex (McKenna, 1968, figs. 3, 4; Sigé, 1976, figs. 2, 95); however, the Late Paleocene *Praolestes* from Mongolia (Lopatin *et al.*, 2001) has a coronoid process of the soricid type.

The ascending ramus of the mandible at the level of the lower sigmoid incisure of *Soricolestes*, longer than that of other soricids, and the shallow incisure between the angular process and the lower edge of the horizontal ramus should be regarded as primitive characters.

THE ORIGIN OF THE SORICIDAE

Soricolestes extends the known history of shrews for at least 5 Ma. The morphological features of the mandible and teeth of *Soricolestes* allow one to evaluate the hypotheses of the origin of the Soricidae from a new point of view.

It is generally believed that, among extinct soricomorph insectivores, the Paleogene Holarctic family Nyctitheriidae is especially close to the Soricidae. Simpson (1945) considered nyctitheriids to be a group of primitive shrewlike soricoids lacking the most important adaptations of the Soricidae. Saban (1958), Gureev (1971, 1979), and Sigé (1976) tentatively associated the origin of soricids with Eocene nyctitheriids. Simpson, Saban, and Gureev placed the nyctitheriid genus *Saturninia* Stehlin, 1940 from the Late Eocene and Early Oligocene of Europe in the Soricidae; Gureev ranked it as a separate subfamily, Saturniniinae Gureev, 1971, opposed to all other shrews, which he referred to the Soricinae. Repenning (1967) excluded *Saturninia* from the Soricidae and did not consider the Nyctitheriidae to be the ancestral group of shrews (mainly because of the presence of a molariform P_4 in nyctitheriids).

Van Valen (1967) proposed that the Soricidae could originate from the Plesiosoricidae or Adapisoricidae (including nyctitheriids in the latter family). Butler (1988) hypothesized that the Soricidae and Nyctitheriidae (which he considered to include *Leptacodon*, *Plagiogtendon*, *Nyctitherium*, *Saturninia*, *Scraeva*, and *Amphidozotherium*) are relatively remote (i.e., related only at the level of the Soricomorpha) and that shrews have the nearest common ancestor with the Plesiosoricidae.

Reumer (1987) proposed that the Heterosoricidae and the Soricidae independently evolved from the Eocene Nyctitheriidae and that the more primitive Heterosoricidae diverged from the common stock earlier than the Soricidae.

Morphological differences between nyctitheriids and all previously known shrews are rather great. In contrast to the Soricidae, nyctitheriids are characterized by a long mandible; a deep masseteric fossa; a complete dental formula; usually, a molariform P_4 ; molars with a large and centrally positioned hypoconulid; and an extended M_3 . The main evolutionary changes of nyctitheriids include the shortening of the infraorbital canal, reduction of canines, development of multicuspoid incisors, expansion of the hypocone shelf, and expansion of the jaw condyle; in addition, European genera lost the anterior mental foramen and gained a more vertical position of the coronoid process (Butler, 1988). The trend toward reduction of premolars, progressive demolarization of P_4 , and reduction of the talonid on M_3 , which is observed in some nyctitheriid groups, e.g., in the Late Eocene European Amphidozotheriinae (Sigé, 1976), appeared too late to be associated with the origin of the Soricidae and, consequently, should be regarded as an example of parallel development.

The structure of the lower molars of *Soricolestes* is characteristic of shrews; at the same time, this form is intermediate between the Nyctitheriidae and typical Soricidae with reference to certain important morphological characters: the only weakly reduced row of antemolars, which are differentiated into incisors, canine, and premolars; a large and nonspecialized P_4 , with a paraconid, a rudimentary metaconid, and a short talonid; a well-developed hypoconulid on M_3 ; and the primitive structure of the ascending ramus. These characters corroborate the hypothesis of the origin of shrews from Early Paleogene Asian nyctitheriids (Sigé, 1976).

The presently known Nyctitheriidae from Asia comprise the Late Paleocene *Praolestes*, *Jarveia*, and *Bayanulanius*; Early Eocene *Bumbanius* and *Oedolius*; and Middle–Late Eocene *Yuanqulestes* (Russell and Dashzeveg, 1986; Averianov, 1995; Tong, 1997; Meng *et al.*, 1998; Lopatin *et al.*, 2001). In the dental structure, the listed genera clearly differ from *Soricolestes* and, thus, cannot belong to a nyctitheriid group that gave rise to the Soricidae. However, certain characters of M_2 and M_3 of *Soricolestes* are similar to those of a small nyctitheriid that was found in the Bumban Member of the Naran Bulak Formation of the Tsagan-Khushu locality in Mongolia along with *Oedolius perexiguus* and *Bumbanius rarus* (collection housed at PIN). M_2 of this form has a high entocristid and a small hypoconulid positioned close to the entoconid but separated from the latter by a clear fold (one can propose that just such a sublingual hypoconulid was modified

into the entostylid characteristic of shrews). The talonid of M_3 is reduced to a greater extent than in other nyctitheriids (excluding *Amphidozotherium*); regarding the general structure, it is very similar to M_3 of *Soricolestes*; however, it has a relatively larger hypoconulid and entoconid. On the other hand, the complete dental formula, the double-rooted P_2 and P_3 , and the structure of the lower molars suggest close relationships between this member of the Nyctitheriidae and the *Saturninia* lineage; *S. grisollensis* and *S. tobieni* from the Upper Eocene of France (Sigé, 1976, figs. 30, 36, 39) show especially high similarity in the structure of the lower molars. Thus, it may be concluded that, in principle, the entire set of dental characters of the Soricolestinae could have been formed in Late Paleocene–Early Eocene Asian nyctitheriids.

The structure of the mandible and teeth of *Soricolestes* allows one to regard it as the ancestor of all later shrews. This suggests a common origin of the Heterosoricinae and the subfamily Crocidossoricinae, which is ancestral to the other Soricidae. Thus, there is no need to follow the idea proposed by Reumer (1987), who ranked the Heterosoricinae as a separate family. It is worth noting that the nearest common ancestor of the Heterosoricinae and the Crocidossoricinae should be more advanced in a number of dental characters than *Soricolestes*; in particular, it should have a relatively short antemolar row and more reduced P_4 and M_3 . Apparently, the divergence of the Heterosoricinae from the Soricolestinae occurred rather early; as early as the end of the Middle Eocene, they had formed a specialized shrew group, which retained a primitive structure of the ascending ramus of the mandible. The Crocidossoricinae probably appeared in Asia in the Middle–Late Eocene.

In conclusion, it may be noted that *Soricolestes soricavus* was the smallest insectivore from the Khaychin Fauna. Judging from the measurements of the mandible and teeth, *Soricolestes* was of approximately the same size as the Recent common shrew (*Sorex araneus* L.). Apparently, the ecological type of the Soricidae was initially formed as the smallest size class of insectivores.

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